A Model of Biofilm Detachment

Philip S. Stewart*
Center for Interfacial Microbial Process Engineering, College of Engineering, Montana State University, Bozeman, Montana 59717

Received May 12, 1992/Accepted August 6, 1992

A general mathematical framework for modeling biofilm detachment is presented. The approach is founded on a material balance on biomass that equates the detachment rate to the product of a detachment frequency and a detaching particle mass. The model provides a theoretical basis for deriving many of the empirical detachment rate expressions in common use and can thus lend some insight into their physical and biological significance. By allowing for variation in the detachment frequency with depth in the biofilm, the model permits derivation of detachment expressions that reflect a dependence on chemical or physiological gradients in the biofilm. Analysis of literature data sets from two different biofilm systems suggests, in both cases, that detachment is a growth-associated phenomenon.
Key words: biofilm • detachment • model • physiology

INTRODUCTION

Biofilm detachment refers to the interphase transport of biomass particles from an attached microbial film to the fluid compartment bathing the film. Although detachment has not been investigated extensively, it is the primary process that balances microbial growth and, thereby, determines the steady state accumulation of biofilm and overall biofilm activity. To the extent that detachment influences attached microbial numbers, it is crucial to understanding such phenomena as microbial plugging of oil formations, fouling of process water equipment, in situ bioremediation, souring of oil by sulfate-reducing bacteria, and the effectiveness of biocides in removing microbial biofilm. Detachment of multicellular particles may also play a role in the development of biofilm spatial heterogeneity or "patchiness," which has been hypothesized to be a factor in the promotion of microbially induced corrosion. Finally, detachment may provide an inoculum for growth of a suspended cell population. This mechanism may underlie recurrent coliform infections in drinking water distribution systems or the persistence of certain microbial infections stemming from medical implants.

Bryers has distinguished five categories of detachment processes: erosion, sloughing, human intervention, predator grazing, and abrasion.[4] Erosion refers to the removal of individual cells or small groups of cells from the surface of the biofilm. Sloughing, in contrast, is the detachment of relatively large particles of biomass, whose characteristic size is comparable to or greater than the thickness of the biofilm itself. Whereas erosion can be viewed as a continuous process occurring uniformly over the surface of a biofilm, sloughing is more plainly a discrete process. The distinction between erosion and sloughing may be arbitrary since many systems probably experience detachment of a broad distribution of particle sizes. Erosion and sloughing have been hypothesized to result from a combination of internal biofilm processes and shear and normal forces exerted by moving fluid in contact with the biofilm surface.[8] Other detachment processes, such as human intervention (e.g., scraping), predator grazing, and abrasion, are clearly the result of external forces acting on the biofilm. This article focuses on erosion or sloughing processes that occur even in the absence of these external forces.

A variety of empirical mathematical expressions to describe detachment rates have been forwarded. One commonly applied detachment model assumes a first-order dependence of detachment rate on biofilm mass and thickness[6,12,13]:

$$r_{di} = k_d \rho_i L_f \tag{1}$$

where

r_{di} = detachment rate of component i
k_d = detachment rate coefficient
ρ_i = density of component i in the biofilm
L_f = biofilm thickness

Others have postulated that detachment rate is a power law[2] or second-order function[5,9] of biofilm mass. For example,

$$r_{di} = k_d(\rho_i L_f)^2 \tag{2}$$

A second-order function of biofilm thickness has been used to model biofilm detachment in a numerical simulation of multispecies population dynamics[17]:

$$r_{di} = k_d \rho_i L_f^2 \tag{3}$$

Shear stress has been explicitly incorporated in some detachment rate expressions. Based on an analysis of limited data, Rittman suggested

$$r_{di} = k_d \rho_i L_f \tau^{0.58} \tag{4}$$

where τ is the fluid shear stress.[13] A first-order dependence on shear stress of the form

$$r_{di} = k_d \tau \rho_i \tag{5}$$

has also been proposed.[1]

* To whom all correspondence should be addressed.

Biotechnology and Bioengineering, Vol. 41, Pp. 111–117 (1993)

CCC 0006-3592/93/010111-07

A few models of detachment postulate a dependence on cellular physiology. Speitel and DiGiano suggested that growth rate in the biofilm influences detachment rates and have proposed an expression of the form[15]

$$r_{di} = L_f(k_d + k'_d\mu) \tag{6}$$

Chang et al. also allude to the possibility of a functional dependence of detachment on growth rate.[7] Howell and Atkinson presented a detachment model in which oxygen depletion in the depth of the biofilm triggers a sloughing event.[10]

While these various detachment models can sometimes adequately describe behavior in a given experiment, there is no convincing evidence that any of the expressions are generally applicable. The objective of this article is to present an improved mathematical basis for modeling of biofilm detachment and prediction of steady state biofilm thickness or areal mass density. A central hypothesis motivating this work is that the probability of a detachment event occurring can be a function of local cellular physiology in the biofilm and could, therefore, vary spatially and temporally depending on the current physiological conditions. A second motivation is the recognition that a mathematical description of detachment should incorporate the inherently discrete nature of this process. A biofilm detachment model that addresses these issues is presented in the next section.

THEORY

Consider a biofilm in which a detachment event can occur at any depth in the film, spawning detached particles of varying size (Fig. 1). One conceptual approach to modeling this process is to equate the detachment flux to the product of the frequency or probability of detachment events and the size or mass of the detaching particle. According to this conceptual model, the average areal detachment rate for component i could be mathematically expressed as

$$r_{di} = F_d(L_f - z_d)A_d\rho_i \tag{7}$$

where F_d is the overall frequency of detachment events per unit area, $L_f - z_d$ is the average depth at which detachment occurs in the biofilm, A_d is the average area of the particle [such that $(L_f - z_d)A_d$ equals the particle volume], and ρ_i is the particle average biofilm density of component i. The detachment rate r_{di} has units of $ML^{-2}T^{-1}$ (M = mass, L = distance, T = time). The overall frequency of detachment, which has units $T^{-1}L^{-2}$, could be a function of biofilm thickness, fluid shear stress, microbial physiology, etc.

This conceptual model may be refined by permitting the detachment frequency to vary with depth in the biofilm. The local detachment frequency might depend, for example, on the physiological state of cells at different points within the biofilm. To obtain the overall detachment rate, the local detachment frequency must be integrated across the depth of the biofilm. With a spatial coordinate, z, defined as originating at the substratum–biofilm interface and oriented outward normal with respect to the plane of the biofilm, the areal rate of detachment can be expressed as

$$r_{di} = \int_0^{L_f} f_d(z)\,(L_f - z)A_d\rho_i(z)\,dz \tag{8}$$

In this expression, $f_d(z)$ denotes the local detachment frequency and $\rho_i(z)$ the local density of component i. The local detachment frequency has units of $T^{-1}L^{-3}$, or frequency per unit volume. The dimension of the detaching piece when detachment occurs at distance z is $L_f - z$. The overall detachment frequency is given by

$$F_d = \int_0^{L_f} f_d(z)\,dz \tag{9}$$

By assuming a form for $f_d(z)$ and integrating Equation (8), various expressions for the detachment rate can be derived. Two general assumptions are made in the derivations that follow. First, it is assumed that biofilm density is spatially and temporally constant for a given system and set of operating conditions. Biofilm density may vary, however, from experiment to experiment. Second, $f_d(z)$ is assumed to be inversely proportional to the contact area of the detaching particle, A_d. The justification for this assumption is that the adhesive force acting on the particle so as to resist detachment could be expected to be proportional to the contact area. A number of possible expressions for $f_d(z)$ are considered below.

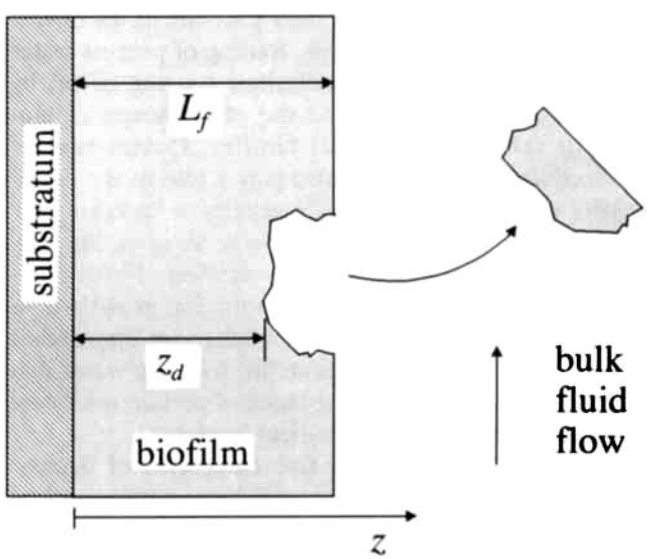

Figure 1. Schematic of biofilm detachment. The diagram illustrates detachment of a particle of biomass and its entrainment in the fluid compartment. In the coordinate system adopted, the substratum is located at $z = 0$ and the biofilm–fluid interface at $z = L_f$. The particle shown detaches at distance $z = z_d$.

Perhaps the simplest form of the local detachment frequency is to assume that it is constant throughout the biofilm:

$$f_d(z) = \frac{k_d}{A_d} \tag{10}$$

where k_d is a detachment coefficient with units $T^{-1}L^{-1}$. Integrating Equation (8) with this form of $f_d(z)$ yields

$$r_{di} = \frac{1}{2}k_d\rho_i L_f^2 \tag{11}$$

This model predicts a second-order dependence of detachment rate on biofilm thickness. As discussed in the next paragraph, this model assures a steady state.

For a biofilm to attain steady state, the net rates of detachment and growth must exactly balance. The rate of biomass synthesis is expected to be first order in the amount of biomass, except when mass transfer limits growth, a common occurrence in biofilms. When mass transfer limits growth, the rate of synthesis will be less than first order in the amount of biomass. In general, then, the rate of biomass synthesis will always be between zero order and first order with respect to L_f. For a biofilm to develop, the rate of detachment must be less than the rate of synthesis for biofilms thinner than steady state thickness and must exceed the rate of synthesis for biofilms thicker than steady state thickness. This requires that the rate of detachment have a higher order dependence on L_f than the rate of growth does. Any detachment rate expression that tends to zero for infinitesimally thin biofilms and that has at least a first-order dependence on L_f, such as Equation (11), will ensure a finite steady state.

In contrast to the previous example, in which the detachment events are distributed throughout the biofilm, it is also conceivable that detachment tends to occur at a preferred location in the biofilm. This dependence of the local detachment frequency can be mathematically formulated in terms of the Dirac delta function, $\delta(z)$,

$$f_d(z) = \frac{k_d\,\delta(z - z_d)}{A_d} \tag{12}$$

where z_d is the value of z at which detachment occurs. The local detachment frequency is zero elsewhere within the biofilm. This leads to the following equation for the detachment rate:

$$r_{di} = k_d\rho_i(L_f - z_d) \tag{13}$$

For example, if detachment occurs by sloughing solely at the biofilm–substratum interface, then $z_d = 0$, and the detachment rate is first order with biofilm thickness. If detachment were to occur at a fixed distance from the biofilm surface ($L_f - z_d = \text{const}$), then Equation (13) would predict that the detachment rate would be constant. This situation does not permit a finite steady state. Detachment would outweigh growth in an arbitrarily thin film, causing the film to disappear.

A connection to microbial physiology in the biofilm can be introduced by postulating that $f_d(z)$ depends on the local growth rate. This can be generally framed as

$$f_d(z) = \frac{k_{d1}\mu(z) + k_{d2}}{A_d} \tag{14}$$

where $\mu(z)$ describes the growth rate as a function of position in the biofilm. Two independent detachment coefficients, k_{d1} and k_{d2}, appear in this expression. Depending on the sign of k_{d1}, Equation (14) can describe either a positive or negative dependence on growth rate. From Equation (8), the detachment rate is predicted to be

$$r_{di} = k_{d1}\rho_i\int_0^{L_f}\mu(z)\,(L_f - z)\,dz + \frac{1}{2}k_{d2}\rho_i L_f^2 \tag{15}$$

Analytic solutions to the integral in Equation (15) are not generally available but can be found for certain special cases, as illustrated below.

The kinetics of microbial growth are frequently described by a Monod expression,

$$\mu = \mu_s\frac{S}{K_s + S} \tag{16}$$

where μ_s is the maximum growth rate of the organism and K_s is the Monod half-saturation coefficient. In the limiting cases of low or high substrate concentration, the growth rate becomes first order in substrate ($S \ll K_s$) or zero order in substrate ($S \gg K_s$). First- and zero-order kinetic expressions thus constitute informative bounds on the growth behavior of microorganisms.

For the case of zero-order intrinsic growth kinetics, the growth rate is finite and constant over a fixed depth from the biofilm–fluid interface and zero at greater depths. Let μ_s denote the growth rate within the growing region and a the dimension of this zone. Then from Equation (15), the detachment rate equals

$$r_{di} = \frac{1}{2}k_{d1}\mu_s\rho_i a^2 + \frac{1}{2}k_{d2}\rho_i L_f^2 \tag{17}$$

A Thiele modulus, which reflects the relative rates of reaction and diffusion,[11] can be defined for the zero-order intrinsic kinetics case as

$$\phi_0^2 = \frac{\mu_s\rho_x L_f^2}{Y_{xs}D_e S_o} \tag{18}$$

where

ρ_x = cell density in the biofilm
Y_{xs} = yield coefficient of biomass on substrate
D_e = effective diffusivity of substrate in the biofilm
S_o = bulk substrate concentration

When the Thiele modulus is small ($\phi_0 < 1$), diffusion is fast compared to reaction and the growth rate is essentially uniform across the depth of the biofilm. When the Thiele modulus is large ($\phi_0 > 1$), diffusion is rate

limiting, and gradients in the growth rate can be expected.

In the case of first-order growth kinetics, the growth rate mirrors the substrate profile in the biofilm and is given by

$$\mu(z) = \mu_s \frac{\cosh(\phi_1 z/L_f)}{\cosh \phi_1} \tag{19}$$

where μ_s represents the growth rate at the biofilm–fluid interface and ϕ_1 is a Thiele modulus defined as

$$\phi_1^2 = \frac{2\mu_s \rho_x L_f^2}{K_s Y_{xs} D_e} \tag{20}$$

Substituting the form of $\mu(z)$ given by Equation (19) into Equation (15), the detachment rate for first-order kinetics is found to be

$$r_{di} = k_{d1}\mu_s \rho_i L_f^2 \left[\frac{\cosh \phi_1 - 1}{\phi_1^2 \cosh \phi_1}\right] + \frac{k_{d2}\rho_i L_f^2}{2} \tag{21}$$

At steady state, the net rate of synthesis of component i must equal its rate of detachment. If the growth rate profile in the biofilm is known or assumed, then the synthesis rate can be directly calculated by integrating over the depth of the biofilm. In general, the areal rate of production of component i, denoted by r_{pi}, is

$$r_{pi} = \int_0^{L_f} \mu(z)\rho_i dz \tag{22}$$

For zero-order growth kinetics, the rate of synthesis is just

$$r_{pi} = \mu_s \rho_i a \tag{23}$$

Equating Equations (15) and (23) to solve for the steady state biofilm thickness, L_{ss}, one obtains

$$L_{ss} = \begin{cases} \dfrac{2\mu_s}{k_{d1}\mu_s + k_{d2}} & \phi_0 \le 1 \quad (24a) \\ \left(\dfrac{2\mu_s a - k_{d1}\mu_s a^2}{k_{d2}}\right)^{1/2} & \phi_0 > 1 \quad (24b) \end{cases}$$

When first-order growth kinetics apply, the rate of synthesis is

$$r_{pi} = \mu_s \rho_i L_f \frac{\tanh \phi_1}{\phi_1} \tag{25}$$

Equating the rates of synthesis and detachment, the steady state biofilm thickness for the first-order kinetic assumption is given by the equation

$$L_{ss} = \frac{\tanh \phi_1}{\phi_1\left[k_{d1}\left(\dfrac{\cosh \phi_1 - 1}{\phi_1^2 \cosh \phi_1}\right) + \dfrac{k_{d2}}{2\mu_s}\right]} \tag{26}$$

Equation (26) is an implicit equation since ϕ_1 is also a function of biofilm thickness.

The above examples by no means exhaust the possible expressions that could be postulated for $f_d(z)$ and subsequently derived for the detachment rate. They do comprise a spectrum of interesting predictions, which are discussed and compared to available data in the next section.

RESULTS AND DISCUSSION

Derived detachment rate expressions are summarized in Table I. All of the expressions are first order in biofilm cell mass density, and most also incorporate some dependence on biofilm thickness. A second-order dependence of the detachment rate on biofilm thickness emerges in several of the rate expressions or their asymptotic limits. In the conceptual terms of the proposed model, this dependence results if both the overall frequency of detachment events and the average size of the detaching particle are proportional to L_f. When some dependence on local growth rate is assumed, the overall dependence of detachment rate on biofilm thickness is predicted to vary between independence and second order.

Only one of the derived detachment rate expressions [Equation (13), $z_d = 0$] embodies simple first-order de-

Table I. Summary of derived detachment rate expressions.

Conceptual description of local detachment frequency	Equation	Dependence of r_{di} on L_f	Steady state?
Uniform	11	L_f^2	assured
Detachment solely at substratum	13, $z_d = 0$	L_f	for $\phi > 1$
Surface erosion of particles of fixed dimension	13	none	no
Generally growth proportional	15	varies; none to L_f^2	permitted; assured if $k_{d2} > 0$
Strictly growth proportional, zero-order growth kinetics	17, $k_{d2} = 0$	L_f^2	for $\phi_0 \le 1$
Strictly growth proportional, first-order growth kinetics	21, $k_{d2} = 0$	L_f^2, small ϕ; none, large ϕ	permitted

pendence on biofilm thickness. This form was derived by assuming that detachment occurs only at the substratum–biofilm interface. The size of the detaching particle is clearly first order in L_f, while the overall frequency of detachment events must be constant. This expression applies only to this specific detachment process, which might be classified as sloughing. A detachment rate first order in L_f could also arise if an external force, such as abrasion, drives detachment. In this case, it is reasonable to postulate that the frequency of detachment events is independent of biofilm thickness. As noted in the introduction, this latter case is not the focus of this article.

Most of the derived detachment rate expressions permit a steady state with respect to biofilm thickness. Material balance considerations lead to the steady state condition which requires that the detachment rate equal the net synthesis rate. Although some biofilm systems may never operate at steady state, it is a general observation that most biofilm processes do attain a (pseudo) steady state. One model, in which it was assumed that particles of constant thickness detach from the surface of the biofilm [Equation (13), $L_f - z_d = \text{const}$], does not permit a steady state, which is sufficient grounds for dismissing it as a generally applicable model. If detachment is a first-order function of biofilm thickness, a finite steady state can only be realized if there is some reduction of biofilm growth by mass transfer limitation.

Those models which assume that detachment is purely growth associated [Equation (15), $k_{d2} = 0$] lead to an intriguingly simple prediction of the steady state biofilm thickness under certain conditions. In the case of zero-order kinetics, if the biofilm is fully penetrated by substrate, then the steady state biofilm thickness is predicted to be constant and equal to $2/k_{d1}$ [Equation (24a), $k_{d2} = 0$]. In other words, the steady state biofilm thickness is uniquely determined by a biological property of the system (embodied in k_{d1}) and is independent of bulk substrate concentration, biofilm density, effective diffusivities, and other physical and chemical properties of the system. The identical result appears in the case of first-order kinetics if ϕ_1 is small [Equation (26), $k_{d2} = 0$, $\phi_1 < 1$]. These results suggest that, for growth-associated models of detachment, when the effectiveness factor is close to 1, or equivalently when the generalized Thiele modulus is less than 1, then the steady state biofilm thickness will be constant. This theoretical result could explain observations of a biofilm system in which biofilm thickness remained constant even as the cell density in the biofilm changed significantly.[3]

There is a general lack of detachment rate data complete enough to test such models of detachment. Consider, for example, that data reported by Trulear and Characklis[16] have been interpreted as supporting both a first-order[13] and second-order[9] dependence of detachment rate on biofilm mass (i.e., $\rho_i L_f$). This article forwards, in the following paragraphs, a third interpretation of this same data set.

Trulear and Characklis collected comprehensive measurements on a heterotrophic mixed population biofilm.[16] As noted above, these data have been analyzed previously, but these analyses considered only a subset of the available data (Trulear, M. G., 1980. Dynamics of biofilm processes in an annular reactor. M.S. Thesis, Rice University). When the entire data set is examined, neither first- nor second-order dependence of the detachment rate on biofilm mass appears defensible. If the simple model $r_{di} = k_d \rho L_f$ were obeyed, a plot of r_{di}/ρ versus L_f would be a straight line with positive slope and passing through the origin. The data clearly do not support this prediction, a conclusion that Figure 2 drives home forcibly. A second-order model does not describe the data any better (data not shown).

In addition to measurements of detachment rate, thickness, and biofilm mass, Trulear and Characklis presented evidence that the intrinsic kinetics of substrate utilization could be considered zero order and reported an experimental measurement of the active biofilm thickness. This additional data make it possible to directly test the growth-associated model of detachment reflected in Equation (17). To do this, Equation (17) is linearized by dividing through by $\rho_i L_f^2/2$. Restricting the analysis in the first round to steady state measurements, r_{di}/ρ_i can be substituted for μa from Equation (23). A plot of $2r_{di}/\rho_i L_f^2$ versus $r_{di}a/\rho_i L_f^2$ should then be linear with slope k_{d1} and intercept k_{d2}.

Trulear and Characklis' steady state data are presented in this manner in Figure 3. The data are linear on this plot to a good approximation ($r^2 = 0.98$). From the least-squares fit line, the detachment constants and their standard errors are found to be $k_{d1} = 0.032 \pm 0.002\ \mu\text{m}^{-1}$ and $k_{d2} = 0.0003 \pm 0.0003\ \mu\text{m}^{-1}\ \text{h}^{-1}$. As a further test of this model, these detachment coefficients can be used to predict the unsteady state accumulation of biofilm. The predicted detachment rate as a function of biofilm mass is compared to the experimental mea-

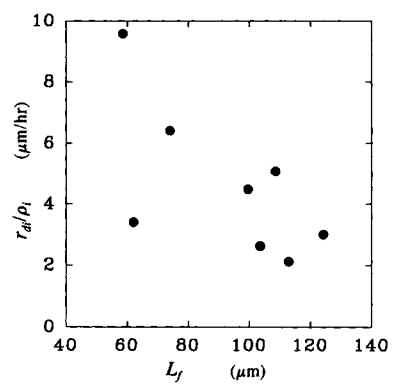

Figure 2. Dependence of detachment rate/biofilm density (r_{di}/ρ_i) on biofilm thickness (L_f) for steady state data (eight experiments) of Trulear and Characklis.

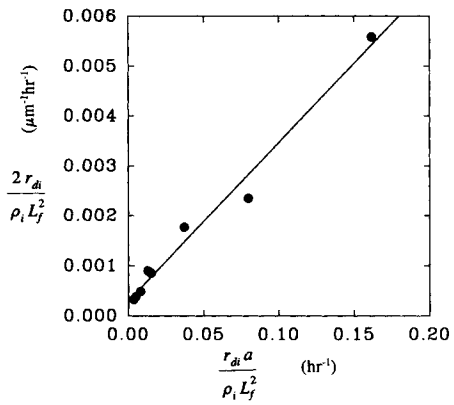

Figure 3. Derivation of detachment constants from steady state data of Trulear and Characklis.[16] Shown are the data (●) (steady state values from eight experiments) and their least-squares fit line (——).

surements in Figure 4. The model correctly predicts the qualitatively distinct behavior of the two experiments.

A second extensive detachment data set has been collected over a period of years by several different experimenters working with pure culture *Pseudomonoas aeruginosa* biofilms.[2,14] This and additional, as yet unpublished, data have recently been analyzed to determine which of several possible detachment rate expressions provided the best fit of the data (Peyton, B., Characklis, W., A statistical analysis of the impact of substrate utilization and shear stress on the kinetics of biofilm detachment, submitted to *Biotechnol. Bioeng.*). The following empirical equation best described the data:

$$r_{di} = k_d \frac{Q}{A}(S_i - S_o)Y_{xs}L_f \tag{27}$$

where $Q(S_i - S_f)/A$ is the areal substrate utilization rate in the reactor. If the reactor system is close to steady state with respect to substrate concentration, a good approximation for essentially all of the experimental measurements, then

$$QY_{xs}(S_i - S_o) = A\bar{\mu}\rho_i L_f \tag{28}$$

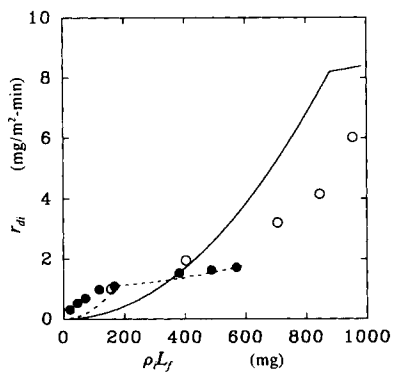

Figure 4. Comparison of model predictions with unsteady state detachment rate data of Trulear and Characklis.[16] Detachment rate (r_{di}) is plotted as a function of biofilm mass ($\rho_i L_f$). Shown are the data (●) and theory (---) for their experiment AFR-26 and data (○) and theory (——) for experiment AFR-23.

where μ is the average specific growth rate in the biofilm. Combining Equations (27) and (28) yields

$$r_{di} = \frac{k_d \bar{\mu} \rho_i L_f^2}{2} \tag{29}$$

This is a special case of Equation (15), the general expression for growth-associated detachment derived here. Equation (15) reduces to Equation (28) if all detachment is growth associated ($k_{d2} = 0$) and if the growth rate in the biofilm is approximately constant ($\phi < 1$). Thus, the proposed model provides theoretical support for an originally empirical detachment equation.

Both of the data sets discussed above support the hypothesis that microbial physiology plays a role in determining detachment rates. Proving this association requires a more extensive set of measurements than is usually collected. In addition to measurements of detachment rate, biofilm thickness, and biofilm mass, sufficient additional information is needed to calculate growth rate profiles within the biofilm. A general implication of growth-associated detachment is that steady state biofilm thickness is less dependent on the amount of growth occurring than when detachment is not related to growth. The best way to test for growth-associated detachment is to vary the amount of net growth occurring, for example, by changing the substrate loading rate. Further experimental investigation will be necessary to establish the ways in which microbial physiology in biofilms influences detachment. An advantage of the model described here is that it permits a dependence on the local physiology in the biofilm to be explicitly included in the detachment rate expressions.

In addition, the model structure incorporates the discrete nature of biofilm detachment. Although not developed in this article, it would be straightforward to expand the model to a second dimension to describe phenomena in the plane of the biofilm. In principle, such an expanded model could describe variations in biofilm thickness, sometimes termed "patchiness" or roughness, and predict the size distributions of detaching biomass particles.

CONCLUSIONS

A general mathematical framework for modeling biofilm detachment is presented. After preliminary analysis of the model and two experimental data sets, it is concluded that:

1. The proposed detachment model provides a theoretical basis for deriving many of the empirical detachment rate expressions in common use and can, thus, lend some insight into their physical and biological significance.
2. By allowing for variation in the detachment frequency with depth in the biofilm, the model permits derivation of detachment expressions that reflect a

dependence on chemical or physiological gradients in the biofilm.

3. The structure of the model incorporates the discrete nature of the detachment process. This should allow the model to be extended to predict heterogeneity in biofilm thickness and the particle size distribution of detached biomass.

Partial support from the National Science Foundation Engineering Research Center Program and the Center Industrial Associates is gratefully acknowledged. The author thanks B. Peyton for early communication of research results and B. Peyton, W. Drury, D. Chen, and W. Characklis for their comments on the manuscript.

NOMENCLATURE

a	depth of growing region
A	total biofilm area
A_d	effective area of detaching particle
D_e	effective diffusivity of substrate in biofilm
f_d	local detachment frequency
F_d	overall detachment frequency
k_d	detachment rate coefficient
k_{d1}	growth-associated detachment coefficient
k_{d2}	non-growth-associated detachment coefficient
K_s	Monod half-saturation coefficient
L_f	biofilm thickness
L_{ss}	steady state biofilm thickness
Q	flow rate
r^2	correlation coefficient squared
r_{di}	detachment rate of component i
r_{pi}	rate of synthesis of component i
S	substrate concentration
S_f	influent substrate concentration
S_o	bulk substrate concentration
Y_{xs}	yield coefficient of cell mass on substrate
z	distance coordinate
z_d	average distance at which detachment occurs

Greek letters

δ	Dirac delta function
μ	specific growth rate
μ_s	specific growth rate at the biofilm–fluid interface or maximum specific growth rate
μ	average specific growth rate in biofilm
ρ_i	density of component i in biofilm
ρ_x	cell mass density in biofilm
τ	fluid shear stress
ϕ_0	Thiele modulus, zero-order kinetics
ϕ_1	Thiele modulus, first-order kinetics

References

1. Bakke, R., Characklis, W.G., Turakhia, M.H., Yeh, A.-I. 1990. Modeling a monopopulation biofilm system: *Pseudomonas aeruginosa*. pp. 487–522 In: W.G. Characklis and K.C. Marshall, (eds.), Biofilms. Wiley, New York.
2. Bakke, R., Trulear, M.G., Robinson, J.A., Characklis, W.G. 1984. Activity of *Pseudomonas aeruginosa* in biofilms: Steady state. Biotechnol. Bioeng. **26**: 1418–1424.
3. Bakke, R. Biofilm detachment. 1986. Ph.D. Thesis, Montana State University, Bozeman, MT.
4. Bryers, J.D. 1988. Modeling biofilm accumulation. pp. 109–144 In: M.J. Bazin and J.I. Prosser (eds.), Physiological models in microbiology, vol. 2. CRC, Boca Raton, FL.
5. Bryers, J.D. 1984. Biofilm formation and chemostat dynamics: Pure and mixed culture considerations. Biotechnol. Bioeng. **26**: 948–958.
6. Chang, H.T., Rittman, B.E. 1988. A comparative study of biofilm on activated carbon. J. Water Pollut. Control Fed. **60**: 362–368.
7. Chang, H.T., Rittman, B.E., Amar, D., Heim, R., Ehlinger, O., Lesty, Y. 1991. Biofilm detachment mechanisms in a liquid-fluidized bed. Biotechnol. Bioeng. **38**: 499–506.
8. Characklis, W.G. 1981. Bioengineering report, Fouling biofilm development: A process analysis. Biotechnol. Bioeng. **23**: 1923–1960.
9. Characklis, W.G., Turakhia, M.H., Zelver, N. 1990. Transport and interfacial transfer phenomena. pp. 265–340 In: W.G. Characklis and K.C. Marshall (eds.), Biofilms. Wiley, New York.
10. Howell, J.A., Atkinson, B. 1976. Sloughing of microbial film in trickling filters. Water Res. **10**: 307–315.
11. Karel, S.F., Libicki, S.B., Robertson, C.R. 1985. The immobilization of whole cells: Engineering principles. Chem. Eng. Sci. **40**: 1321–1354.
12. Kreikenbohm, R., Stephen, W. 1985. Application of a two-compartment model to the wall growth of *Pelobacter acidigallici* under continuous culture conditions. Biotechnol. Bioeng. **27**: 296–301.
13. Rittman, B.E. 1982. The effect of shear stress on biofilm loss rate. Biotechnol. Bioeng. **24**: 501–506.
14. Siebel, M.A., Characklis, W.G. 1991. Observations of binary population biofilms. Biotechnol. Bioeng. **37**: 778–789.
15. Speitel, G.E., DiGiano, F.A. 1987. Biofilm shearing under dynamic conditions. J. Environ. Eng. ASCE **113**: 464–475.
16. Trulear, M.G., Characklis, W.G. 1982. Dynamics of biofilm processes. J. Water Pollut. Control Fed. **54**: 1288–1301.
17. Wanner, O., Gujer, W. 1986. A multispecies biofilm model. Biotechnol. Bioeng. **28**: 314–328.